

ON THE OCCURRENCE AND FOOD HABITS OF CTENOPHORES IN NEW JERSEY INLAND COASTAL WATERS.

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I.

Studies of the plankton organisms of New Jersey inland coastal waters (Fig. 1) which have been in progress since March 1919 reveal interesting facts regarding the occurrence and habits of the ctenophores *Mnemiopsis leidyi* Agassiz, *Pleurobrachia brunnea* Mayer, and *Beroë ovata* Chamisso and Eisenhardt. All three of these forms have been found at times in abundance in New Jersey, but again they may be rare or absent. They must, therefore, be considered as transient visitors to these waters. This paper is presented with the hope that the observations herein recorded may aid in the ultimate solution of some of the problems concerned with the distribution of these comparatively little known animals.

The common comb-jelly or sea walnut of the northeastern coast of the United States, *Mnemiopsis leidyi*, was frequently found by Mayer ('12), off Newport, R. I., in great rafts. It was well known in the Woods Hole region until about 1910 when it practically disappeared and has not since been reported there in numbers.¹ Sumner, Osborn, and Cole ('13), p. 579, report this species as varying from scarce to very abundant throughout the Woods Hole region, where it has been recorded by various observers for every month in the year. It was apparently most abundant here in September and in December. These authors note the irregular occurrence of this ctenophore in different years,

¹ Mr. George M. Gray, Curator of the Supply Department at Woods Hole, informs me in a letter of January 28, 1924, that nearly every year one or two specimens are taken in the winter or in spring. I have been informed that numerous *Mnemiopsis* were found here in September 1924 following an extended period of easterly winds.

it being very abundant during some seasons while absent as in 1904 in others. They state that periods of extreme abundance may occur in winter. Sumner, *loc. cit.*, p. 576, records it in such numbers in Buzzards Bay on November 13, 1907, that the parasitic *Edwardsia leidy* within the ctenophores were very conspicuous as one looked down from the deck of the ship.



FIG. 1. Relief map of southern New Jersey. 1, Barnegat Bay; 2, Little Egg Harbor; 3, Great Bay; 4, Maurice River Cove. The floating laboratory was stationed from 1919-1920 at Edge Cove, due west of Beach Haven, and from 1921 to the present at Seaside Park.

Bigelow ('15) encountered "myriads" of *Mnemiopsis leidy* in the surface waters off the New Jersey coast in July, 1913. He found it generally distributed over the inner half of the continental shelf between Barnegat and Delaware Bay, although none was seen north of Barnegat on this voyage.

Pleurobrachia brunnea nov. sp., was found in great numbers by Mayer ('12), on October 16, 1904, off the coast of New Jersey from Barnegat Inlet north to Sandy Hook. The validity of this form as a distinct species has been questioned by Bigelow ('12 and '15), and is discussed in a later section of this paper.

Mayer ('12) lists *Beroë ovata* as abundant along the coast of the United States as far north as Chesapeake Bay. Hargitt ('04) found it common at Woods Hole in 1901, though seldom taken in numbers.

My own records cover only some of the estuaries on the New Jersey coast and do not include the area of oceanic coastal water investigated by Mayer and by Bigelow. During the six years of my investigations *Pleurobrachia* has been found but twice, *Beroë ovata* for short periods during three seasons, while *Mnemiopsis* has been observed daily for months at a time.

Pleurobrachia brunnea was first found by me October 11, 1920, occurring in vast swarms at the surface of water 1-2 meters deep at the mouth of the Mullica River, Great Bay (cf. Fig. 1). Associated with it were numerous *Mnemiopsis leidyi* and many small medusæ of several species. So numerous were the *Pleurobrachia* that the water for yards around the boat was white as though with foam. The ctenophores were found in greatest abundance in the tidal slick which forms along the eastern end of the old Graveling natural oyster bed at the mouth of the Mullica River. The first observation of them was at 11:15 A.M., with bright sunlight, very light NW. wind, tide one third ebb, water temperature 16.6° C., specific gravity 1.0182.² The majority of the jellyfish were so close to the surface that they could be dipped up in a fingerbowl for examination.

During the afternoon of the same day large numbers of *Pleurobrachia* were found over much of Great Bay, and on October 15th, 6 *Pleurobrachia* and 3 *Mnemiopsis* were taken in 3 minutes towing with a 15-in. net in Little Egg Harbor. On my next visit to the region, three weeks later (November 3 and 4), no *Pleurobrachia* were found in Great Bay or in Little Egg Harbor. Numerous *Mnemiopsis* were obtained in the former region; the temperature was 13° C., specific gravity 1.0234.

Occasional visits have been made during the autumn in subsequent years but no *Pleurobrachia* have been found. From

² All figures for specific gravity are reduced to the basis of distilled water at 4° C. Readings were made with an hydrometer calibrated by the U. S. Bureau of Standards and further checked in some instances by titration of standard sea water obtained from the International Commission for the Investigation of the Sea, Copenhagen. For comparison I have with the aid of Knudsen's Tables transposed Bigelow's salinity figures to specific gravity readings.

all the information I am able to gather this ctenophore appears in New Jersey estuaries for a brief period during October, and then disappears. Mr. Gray informs me that with one possible exception *Pleurobrachia* (supposedly *P. pileus*) was not seen in Woods Hole at all in 1923. That it did not occur in Great Bay during the summer of 1921 I am certain, since our floating laboratory was stationed during this period but a few hundred yards from the place where myriads of these ctenophores were observed in 1920.

My first record for *Beroë* is November 4, 1920, when one half grown specimen was taken in Great Bay; the water temperature was 13° C., specific gravity, 1.0216. No further specimens were seen until October 22, 1921, when 2 large individuals were observed in Little Egg Harbor with temperature of 12.5° C., specific gravity 1.0245. No *Beroë* were found in Little Egg Harbor during the autumn of 1922, nor in Barnegat Bay in the autumn of 1923. A few large specimens were taken in the latter region September 11, 1924, water temperature 16.5° C., and by the close of the month they were abundant. This ctenophore appeared in vast swarms, in the Maurice River, Delaware Bay, about the middle of September 1922 and again at the same time in 1923 and in 1924.³ It was reported that at times during the flood tide the *Beroë* were so abundant as almost to form continuous rafts. In each of these years the ctenophores appeared about the second week in September while the water temperature was above 20° C. and remained very abundant until early in October when they disappeared as quickly as they had come.

My records of *Mnemiopsis* are much more extensive than in the case of the two preceding ctenophores. The data illustrate in a striking way what other investigators have noted regarding the intermittent appearance of the sea walnut. During the summers from 1908 to 1917 I frequently noted the presence of *Mnemiopsis*, but being occupied with other problems kept no record of its occurrence. From early in 1919 to the present careful records have been kept of the appearance and relative abundance of the ctenophores. Search for these organisms has

³ I am indebted to two of our former students, Mr. C. A. Perry and Mr. W. H. Dumont, for making these observations and for sending specimens for identification.

TABLE I.

OCCURRENCE OF *Mnemiopsis leidyi* IN NEW JERSEY.

Locality	1919	1920	1921	1922	1923	1924
Little Egg Harbor	Very abundant May to November, 2 qts. obtained in 20 min. tide flow with 15 in. net.	Very scarce during summer. Three taken in 5 min. tide flow on Nov. 4th, temp. 10.6° C. None Nov. 19, temp. 6° C.	None in net in 2 hrs. tide flow May and September. Two caught in a Urosalpinx trap.	None found.	None May 7th; Fairly abundant in late August, remainder of season not known.	Few seen July 24-25. Remainder of season not known.
Great Bay	Not known.	Scarce during summer. Numerous on Oct. 11th with Pleurobrachia. Eight taken in 2 min. tide flow November 3.	None found.	None found.	Occasional specimen seen in late August, Remainder of season not known.	Numerous July 24th. Remainder of season not known.
Barnegat Bay	Not known.	Not known.	Scarce. One specimen 10 cm. long taken in lower Bay Aug. 31. Hit 1 about every 300 ft. at night with launch.	None found. Hit 1 occasionally at night.	Appeared suddenly June 21, specimens of medium size. Increased rapidly and occurred in swarms throughout summer and fall. Very abundant in December, scarce in January, disappeared during February.	Six specimens seen July 3. Great swarms July 8-18.

been made by nets, by traps, and, perhaps best of all where they are scarce, by running a motor boat at night and counting the number of individuals flashing in the wake of the boat. Much of the region covered by these observations is so shallow that the disturbance from a launch's propellor reaches quite to the bottom.

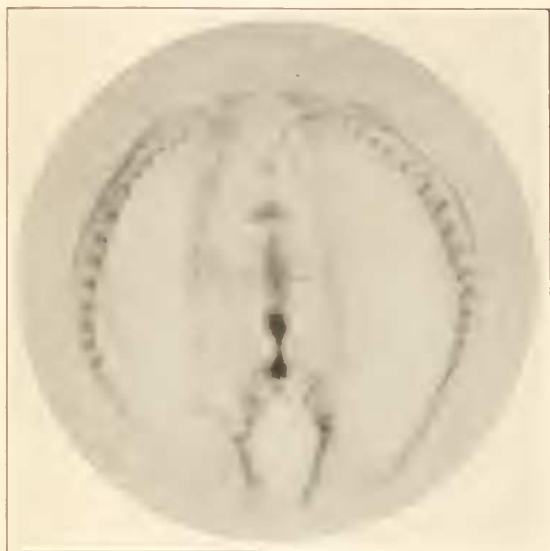


FIG. 2. Young *Mnemiopsis* 5 mm. long in the *Pleurobrachia* stage showing retracted tentacles.

In Table I, a summary is given of our observations of *Mnemiopsis* for the past six years.

Barnegat Bay (*cf.* Nelson, '23:1) is a shallow estuary with an average tidal fluctuation of 4-6 inches. It therefore warms up rapidly in the spring and presents during the summer subtropical temperature conditions. The temperature of the water on June 21, the date of the first appearance of *Mnemiopsis* here in 1923, ranged from 24.5° to 26.1° C. at 7 stations. The specific gravity varied between 1.0117 and 1.0152. The ctenophores which swarmed in the waters of the bay during July, August and September were mostly of medium or of large size.

As the temperature fell with early autumn particular attention was paid to the stage of development of the animals. All specimens taken October 6, at a temperature of 14° C., were

medium or large. On my next visit, October 20, temperature 15° C., I found several great rafts of *Mnemiopsis* about two thirds of the individuals being approximately 5 mm. long. Among these there were both *Pleurobrachia* and *Bolinopsis* stages of development, bearing strong tentacles (Fig. 2). The smallest were not more than a millimeter long. As indicating the abundance of the animals, one 450 cc. fingerbowl dipped up full of the surface water contained in all 36 young *Mnemiopsis* of which 24 were in the *Pleurobrachia* stage and 12 in the *Bolinopsis* stage. The majority of specimens found on subsequent visits during November, December and January were in the *Pleurobrachia* stage, relatively few large specimens being taken.

In the summer of 1924 the first specimens, 6 of medium size, were found July 3, water temperatures 21.5 – 22.7° C. Few were observed after this until the 8th when, with temperatures of 24.5 to 24.9° C, the water was literally alive with *Mnemiopsis*. Most of these were newly hatched embryos corresponding to Mayer's Fig. 35 (Mayer, '12, Pl. 6) which represents an embryo of about 30 hours.

Following this heavy spawning of July 6–8 the water swarmed with the ctenophores, numbers as high as 100 per cubic meter being recorded. The animals continued abundant for about 10 days after which they diminished rapidly in numbers, and at no time after this did they approximate the swarms seen in 1923.

The lower limit of temperature at which *M. leidyi* will breed must be very close to freezing, as the following observations show. The fall of 1923 and January 1924 were very mild; our self-registering water thermograph on the Maurice River, Delaware Bay, rarely fell below 5° C. until late in December. The first freeze in Barnegat Bay occurred on the night of January 5th, the bay being covered with ice for about three days. On the morning of January 5, with a temperature of 2° C., numerous medium and small *Mnemiopsis* were procured.⁴

On my next visit to the region, January 19, no specimens were taken in repeated hauls in the open bay. Medium and very small individuals were fairly abundant, however, in two artificial harbors about 2 meters deep which communicate with the bay by

⁴ I am indebted to Mr. Wible of the Physiology Department of Rutgers University for this observation.

narrow outlets. Although these harbors had been frozen over from the 5th of the month until about a week before my visit, the quietness and depth of the water had apparently provided conditions more favorable to survival of the ctenophores than obtained in the open bay. In horizontal hauls of 8 meters each with a net 1 meter square, as high as 19 *Mnemiopsis* were procured per haul. Of these approximately 90 per cent. were in the *Pleurobrachia* and *Bolinopsis* stages and must have come from eggs liberated since the cold weather early in the month.

No further visits were made to the region until March, since the harbors and much of the bay were ice bound from late January until the close of February. On March 8, 1924, water temperature, 3.5°C ., no *Mnemiopsis* were found. The adverse conditions resulting from the heavy freezing had evidently destroyed the few survivors in the harbors where they were found on January 19th. The disappearance of *Mnemiopsis* from Little Egg Harbor in November and from the open waters of Barnegat Bay early in January is believed to be due chiefly to the effects of heavy storms which raise much sand and debris from the bottom.

III.

THE BEHAVIOR OF *Mnemiopsis* AT LOW TEMPERATURES.

Parker '05 found while working with *M. leidyi* during the summer at Woods Hole, that partial cessation of the paddle plates occurred by chilling to 8.5°C ., with complete loss of movement at 5°C . The absence of movement at this temperature was shown to be due to causes other than the failure of nervous transmission. If 5°C . represented the temperature below which, in their natural environment, movement of the paddle plates of *Mnemiopsis* ceased, the organisms would perish before late autumn in New Jersey. The temperature of 5°C . as determined by Parker must represent a minimum only for *Mnemiopsis* adjusted to summer temperatures.

At sunset November 9 with the water temperature of Barnegat Bay at 7.5°C ., large numbers of *Mnemiopsis* of all sizes were found wherever sought. The following night was cold with a sharp north wind. At 8:30 the next morning numerous *Mnemiopsis* were seen swimming actively at the surface near the

floating laboratory in water with a temperature of 3°C . Several animals were at once dipped up to make certain that the swimming plates were actually in motion.

To determine the minimum temperature at which the paddle plates would beat in winter, on January 19, 1924, I took *Mnemiopsis* from the water beside the laboratory at a temperature of 4°C . With the aid of a pack of ice and salt the water containing the animals was cooled down until at -0.7°C . water and ctenophores became a mass of ice.⁵ As the temperature fell the paddle plates continued beating without interruption. Ice crystals formed about the ctenophores, finally enclosing them, yet while half of an animal was solidly embedded in the advancing ice the paddle plates of the free half continued beating as before. Not until the impinging ice crystals actually imprisoned the plates and held them fast did movement cease.

Mayer ('14) emphasized the fact that whereas tropical marine animals commonly live within 5°C . of their temperature of maximum activity and within $10-15^{\circ}\text{C}$. of their upper death temperatures, marine animals of the temperate or arctic regions show but little change in activity within a considerable range of temperatures. Hunter ('04) showed that *Mnemiopsis leidyi* is relatively more resistant to a decrease than to an increase in temperature of the water. The bearing of these observations on the distribution of *Mnemiopsis* in New Jersey will be considered in the last section of this paper.

IV.

THE FOOD HABITS OF CTENOPHORES.

Little is known of the feeding and food habits of ctenophores. Their delicate structure and relatively short life under laboratory conditions, together with their somewhat sporadic appearance within the reach of laboratories, have made investigation of their habits difficult. Mayer ('12) notes that "young *Beroë cucumis*" devours *Pleurobrachia* "with avidity." Bigelow ('15) observed the great impoverishment of the plankton on German Bank due to *Pleurobrachia pileus*, which "when it swarms seems to obliterate or devour almost everything else in the water." Kincaid ('15)

⁵ Moore ('24) observed the beating of the paddle plates of *Mnemiopsis* at -0.6°C . under laboratory conditions.

states that *Pleurobrachia* may be a serious enemy of the oyster in Washington waters through the large numbers of the larvæ of the latter which it consumes.

In a recent work, the most extensive of its kind with which I am familiar, Miss Lebour ('22, '23) describes the food of numerous plankton organisms. She lists *Pleurobrachia* and *Beroë* with *Sagitta* among the miscellaneous feeders of the plankton. Where these two ctenophores occur together *Beroë* may eat large numbers of *Pleurobrachia*, an observation which was also published by Mayer, however, in 1912. The chief food of *Beroë* was found by Miss Lebour to be small crustacea, although she quotes one observation of a *Beroë* full of diatoms, probably *Coscinodiscus*. *Pleurobrachia* was found to subsist mainly upon *Calanus*, crab zœa larvæ, *Sagitta*, other *Pleurobrachia*, *Syngnathus*, young plaice and plaice eggs. I have not had opportunity to determine the food of *Pleurobrachia*. The *Beroë* which were found September 11, 1924, were living chiefly upon *Mnemiopsis*.

The abundance and persistence of *Mnemiopsis* in Barnegat Bay in 1923 gave opportunity to study the food habits of this ctenophore during the seasonal changes of the plankton. A few preliminary examinations demonstrated that at summer temperatures the rate of digestion of food and the ejection of residue is so rapid as to make necessary the examination of the ctenophores immediately upon removal from the water. In most instances the stomodeum was emptied of all its contents in from 20-30 minutes after removal of the animals from their natural surroundings.

The great transparency of this organism makes it possible to identify with a high degree of accuracy the contents of the stomodeum without in any way disturbing the animal. In making the examinations the station launch was anchored in the desired spot in the open bay and the ctenophores were dipped up in a fingerbowl as needed and examined immediately under the binocular.

During the summer the food of *Mnemiopsis* was found to consist chiefly of larval molluscs, copepods and their nauplii, nannoplankton, and detritus, the relative amounts of these being to some extent correlated with their abundance in the plankton. In this connection I wish to lay emphasis upon a fact

which, so far as my knowledge goes, has not hitherto been stressed. The presence of nannoplankton and of organic debris within the ctenophores demonstrates that these animals make use of their ciliated canals for the transport of minute forms in much the same manner as does a bivalve mollusc. The possession of this feeding mechanism makes available to them the nannoplankton which is by far the greatest constituent of the total plankton, a constituent, moreover, which may be mainly unavailable to their larger cœlenterate allies. This may explain, in part, how such vast hordes of ctenophores can exist together for long periods of time (*cf.* Nelson, '22).

Table II. contains a summary of the food organisms found in *Mnemiopsis* during July.

To summarize the data in Table II.: of 65 *Mnemiopsis* examined during July, 75 per cent. had eaten bivalve larvæ, 50 per cent. contained crustacea, 15 per cent. held gastropod larvæ, while 6 per cent. contained detritus and nannoplankton. One specimen about 3 cm. long had eaten 126 early oyster larvæ.

On December 21, of 10 specimens examined 5 contained a total of 26 large *Calanus* and 1 gastropod larva. Examination of the ctenophores at this time and again on January 19, 1924, revealed a most interesting fact regarding digestion in *Mnemiopsis*. Copepods, as is well known, contain large oil globules, representing stored nutriment. In every ctenophore examined during the winter, oil globules derived from the copepods, were found to be deposited in thick rows beneath the paddle plates. Many minute oil globules were seen passing out of the anus, and one specimen was observed in the act of casting out through the mouth a thick rope of oil globules and detritus. Apparently but little of the oil obtained from the crustaceans used as food is metabolized by the ctenophores, at least at low temperatures. The storage of the oil in such large quantities beneath the paddle plates may serve an important function in decreasing the specific gravity of the body. This accumulation of oil at a time when also the density and the viscosity of the water are greatly increased through low temperature, renders the animal capable of suspension in the water with a minimum of activity of the paddle

plates. That the added factor of buoyancy has survival value during the late fall and winter can scarcely be doubted.

TABLE II.

Date.	Total Number Examined.	Oyster Larvæ.		Other Bi- valve Larvæ.		Crust- acea.		Gas- tro- pod Larvæ.		Detri- tus.		Miscel- laneous.
		Larvæ.	<i>Mnemiopsis</i> .	Larvæ.	<i>Mnemiopsis</i> .	Copepods and <i>Nauplii</i> .	<i>Mnemiopsis</i> .	Larvæ.	<i>Mnemiopsis</i> .	Amount.	<i>Mnemiopsis</i> .	
July 12....	11	301	9	2	2	1	1	3	1			
July 13....	49	74	12	58	14	93	35	3	2	Much	2	1 roundworm 1 atax
July 18 ...	14	77	12			21	6	12	7	Much	2	1 prawn, 3 mm.
Total....	65	452	33	60	16	115	42	18	10		4	

An interesting observation illustrates one limitation of *Mnemiopsis* in its ability to capture planktonts. The water was swarming with polychæte larvæ on December 21, but in spite of the fact that many of these larvæ were found entangled in mucus on the oral lobes and on other parts of the bodies of the ctenophores, in no case were any larvæ found within the stomodeum. The wealth of spines which bristle in all directions on the early larvæ of polychætes evidently render their final capture by *Mnemiopsis* difficult if not impossible.

That the food organisms found within the stomodeum of *Mnemiopsis* are actually digested is shown by the presence of numerous empty shells of bivalve and gastropod larvæ, crustacean carapaces, and other non-digestible remains which accumulate near the oral end of the stomodeum.

V.

THE DESTRUCTION OF BIVALVE LARVÆ BY *Mnemiopsis*.

Our records of the abundance of bivalve larvæ and the intensity of "set" in Barnegat Bay for the past 3 years show, after taking into account the effects of all known factors, that there is a close correlation between the abundance of *Mnemiopsis* and the

intensity of shipworm infestation and of oyster sets. In 1921 and in 1922 heavy sets of *Ostrea*, *Teredo*, and *Bankia* occurred. The oyster set in 1921, especially, was the heaviest seen for some years, as high as 1000 oyster spat attaching to one oyster shell (Nelson, '23A). The sudden and heavy outbreak of *Teredo navalis* at the same time (Nelson, '22) gave rise to fears that there might be enacted in eastern waters a repetition of the San Francisco Bay disaster (Kofoed et al., '21). It will be noted in Table I. that *Mnemiopsis* was absent or rare in Barnegat Bay and adjoining waters during 1921 and 1922.

The oyster set in Barnegat Bay in 1923 was a failure commercially. The best set that could be found at the close of the summer was one or two spat on every third oyster shell. The total season's catch on certain experimental shells was only 7 spat as against over 7000 in 1921.

Teredo navalis infested timbers in numbers as great as 100 per cubic inch of wood in 1921, while in 1923 at the same spot only 10 *Bankia* entered a test raft of 1,520 square inches surface. This very light infestation occurred in spite of the prevalence of slightly higher salinities obtaining in the region than were found in 1921. At only one locality, the jetty at the mouth of Barnegat Creek at the lower end of the Bay, could enough *Teredo* be found even for carrying on experiments with them. This jetty has been heavily attacked by borers for some years and was practically destroyed in 1921. Two infested piling were removed from this structure on July 25 and 5 were taken August 31, 1923. They were moored in a small land-locked creek close to the upper end of the bay, far from marine structures, and were used as a source of supply for study of the heterotrichous ciliate *Boveria teredinidi* Nelson, parasitic upon the gill filaments (Nelson, '23B). Throughout the summer and autumn until freezing occurred the borers grew and flourished, thus proving that no natural conditions present in the bay during this period were inimical to the existence of the adults.

The Director of the Committee on Marine Piling Investigations of the National Research Council, Col. Wm. G. Atwood, informed me in a letter of October 23, 1923, that "on the whole shipworm attack on test blocks was much lighter during 1923 than in 1922, although at one or two points it appears to have been as heavy

or heavier." Unfortunately for the purposes of this discussion there are no data as to the relative abundance of *Mnemiopsis* or of other plankton feeders in the several regions.

The relative reduction in numbers of oyster larvæ in 1921 and in 1923 is of interest. For example, on June 25, 1921, the average number of earliest straight hinge oyster larvæ per 100 liters of water, collected at 7 stations on Barnegat Bay, was 36,200. On the 27th, by which time the larvæ were entering on the early umbo stage, the average number of these larvæ was found to have been reduced to 8,700, representing a quite usual percentage of mortality. In 1923, on June 23, at the central collecting station near the middle of the bay where the early oyster larvæ have been first found in abundance for three successive years, there was obtained a total of 60,850 larvæ per 100 liters. Two days later the average of 8 stations showed but 54 of these larvæ remaining per 100 liters, the largest single catch at any one station being 200. So far as known there were present during 1923 no other factors aside from vast swarms of *Mnemiopsis* which were not also operating in 1921.

It is worth while to add a comparison between oyster sets found in Barnegat Bay by late August, 1923, with those at other oyster producing areas of New Jersey. In the Mullica River an excellent set of oysters one week old was found on August 30. At this date only an occasional *Mnemiopsis* was seen. Although no observations were made in this area earlier in the season there is no reason for believing that the ctenophores were more abundant during the preceding 3 weeks, during which time the oyster larvæ would have matured and set, than they were on the date of my observations. In Delaware Bay also the usual oyster set occurred. The waters of this area are so stormy and turbid near the shore that *Mnemiopsis* cannot thrive there, although the much hardier *Beroë* appears there in abundance in September, as already stated.

VI.

DISCUSSION OF SPECIES.

To the student of the Ctenophora it is apparent that certain wide discrepancies occur between the account of the distribution of the three ctenophores discussed in this paper and the commonly

accepted ideas regarding the habitat of these species. All are usually considered as being strictly oceanic forms, and yet I have taken them in waters ranging from one half to less than a third the salinity of their supposed usual environment.

Mayer '12 holds that there are but two dominant species of *Beroë*, *B. cucumis* of cold waters and *B. ovata* of warm water. *B. forskali*, which was found at numerous stations by Bigelow, is believed by Mayer to be but a variety of *B. ovata*. Bigelow ('15) lists *B. cucumis* from 7 stations at some distance from the coast of New England. He does not record it off the New Jersey coast in July, nor does he mention *B. ovata*.

Mayer ('12) notes that the young of *B. cucumis* cannot be distinguished from those of *B. ovata*. In the adult the peripheral network of vessels arising from the meridional canals freely anastomoses in *B. ovata*, remaining distinct in *B. cucumis*.

Pleurobrachia brunnea, a species created by Mayer '12 to receive a ctenophore found off the New Jersey coast in October, 1904, is of somewhat doubtful position. Bigelow ('12) believed this to be so close to *Hormiphora spatulata* Chun, as to be identical with it. In a later publication ('15) he throws still further doubt on the validity of the species, believing it to be well within the limits of *P. pileus*, a ctenophore of wide distribution which he found in great numbers off the New Jersey coast in July 1913.

The characters used by Mayer to establish *P. brunnea* as distinct from *P. pileus* are: the continuation of the 8 meridional canals for a considerable distance downward beyond the ciliary combs; the yellow color of the stomodeum; and the knobs on the ends of the tentacles. It is distinguished from *Hormiphora spatulata* by the knob-like ends of the tentacles; and by the fact that its ciliated combs begin at a greater distance from the apex than in *H. spatulata*.

My own specimens agree in every particular with Mayer's description and figure of *P. brunnea*, the yellow color of the stomodeum and the knob-like ends of the tentacles being quite striking in the living specimens. The downward continuation of the meridional vessels below the ciliary combs is clearly evident in the preserved as well as in the living specimens. In considering Bigelow's belief that this form may lie within the limits of variation of typical *P. pileus* it is well to remember that

Bigelow obtained his specimens off the New Jersey coast in July, whereas Mayer and I found our ctenophores in October. The three distinguishing characters of *P. brunnea* as established by Mayer are clearly evident even to one who is but little familiar with the characteristics of this group. The chief question would seem to be whether this organism should be raised to specific rank, or be included as a variety of *P. pileus* or of *Hormiphora spatulata*. Its appearance in New Jersey coastal waters in October would seem to point to its being essentially a cool water form and hence closer to *P. pileus*.

The range of *Mnemiopsis leidyi* is given by Mayer as from the southern coast of New England south to the Carolinas. It is considered by Mayer to be a ctenophore of the pure sea water along the outer shores; its place being taken in the brackish water by its much smaller relative, *M. gardeni*. Bigelow ('15) agrees with this from his own findings. Nowhere in the accounts of either of these investigators do I find evidence that they made any careful examination of the estuaries of the New Jersey coast for there *M. leidyi* occurs in abundance for months at a time in water of as low as one-third the salinity of the sea or even below this. On one occasion I found it in upper Delaware Bay, just below Stony Point, in water of a specific gravity less than 1.005.

That I have not confused *M. leidyi* with *M. gardeni* will be evident from the following: (1) *M. gardeni* is described by Mayer as being 35-40 mm. in length when mature. I have found *Mnemiopsis* over 100 mm. long in Barnegat Bay. (2) The oral lobes of *M. gardeni* are very small, from one-fifth to one-sixth as long as the body. In all specimens of *Mnemiopsis* which I have seen, excepting only immature individuals not yet fully emerged into the *Mnemiopsis* stage, the oral lappets are much longer than this and they flare widely. (3) My specimens show, when large numbers are together, a decided pinkish hue, not the bluish color of *M. gardeni*. (4) The range for *M. gardeni* as given by Mayer is from Chesapeake Bay to Florida. (5) the striking power of adaptation of our species to low temperatures argues against its being the southern form. (6) I do not find in my specimens the small low discoidal warts on the oral lobes which according to Mayer are characteristic of *M. gardeni*.

VII.

THE DISTRIBUTION OF CTENOPHORES AS EFFECTED BY SALINITY AND TEMPERATURE.

Mayer ('14) has emphasized the superior temperature adjustment of marine animals of the arctic and temperate zones over individuals of the same or of related species in the tropics. *Mnemiopsis leidyi* in Barnegat Bay illustrates this superiority of adjustment in a striking manner. Owing to the topography and small tidal flow of Barnegat Bay, summer temperatures there may rise well above 26° C. During most of the summer of 1923 the water temperature varied between 24 and 25° C., with specific gravity over the region within 4 miles south of Seaside Park ranging from about 1.0110 to 1.0180.

Bigelow ('15) found *Mnemiopsis leidyi* in July in greatest abundance over the inner half of the continental shelf off the New Jersey coast, in water of a specific gravity between 1.0246 and 1.0252. It was not found in the very salt Gulf stream on the one hand nor where the specific gravity fell below 1.0244 at the mouth of Chesapeake Bay, on the other. The upper limit of temperature at which this ctenophore was found was 24.5° C., the lower about 15.5° C.

He gives the range of *Pleurobrachia pileus* as unbroken from Labrador at least to Pamlico Sound. He found it more generally distributed in the coast waters than any other cœlenterate, with local swarms south as well as north of Cape Cod. The warmest water in which it was found was 20.5° C., the coldest about 6° C. The range in specific gravity was from about 1.0241 to approximately 1.0267. Nearly all the specimens taken were from the deeper waters, whereas the majority of *Mnemiopsis* were found in the first fathom. The swarms of *Mnemiopsis* and *Pleurobrachia* were found to be mutually exclusive; never were these two forms taken side by side.

The distribution of *Pleurobrachia* in the deeper waters, together with the lower temperatures observed, indicate that *Pleurobrachia* is adjusted to colder water off the New Jersey coast than is *Mnemiopsis*. The high summer temperatures of the estuaries such as Barnegat Bay form a barrier which it, unlike *Mnemiopsis*, is unable to pass. In the extreme southern part of its range

Pleurobrachia is undoubtedly adjusted to temperatures equal to if not above those found during the summer in Barnegat Bay.

Pleurobrachia brunnea may be a species or subspecies which is delicately adjusted to a narrow range of temperature, since it is found in the inland waterways of New Jersey only during October, and it was taken in the ocean off Barnegat by Mayer during the same month. It is not stated at what depth these were obtained nor is the temperature given. As bearing on Bigelow's finding that *Pleurobrachia pileus* and *Mnemiopsis* were mutually exclusive, it will be remembered that in the swarms observed by me in the Mullica River *P. brunnea* and *M. leidy* were taken together in large numbers at the surface in water dipped up with a fingerbowl.

In conclusion, consideration must be given to the part which salinity and temperature play in the sporadic appearance of the three ctenophores discussed here. A study of all data relating to rainfall, seasonal temperatures, severity of the preceding winter, and other factors, fails to show any correlation between these and the abundance of the ctenophores. The fact that one or two specimens of *Mnemiopsis* have been taken every year at Woods Hole since they ceased to be found there in abundance, and the presence of occasional specimens in Barnegat Bay even during "off" years, indicates that the factors controlling the appearance of the ctenophores probably lie mainly outside the several localities which are considered in this paper.

All ctenophores disappear from the shallow bays during the winter, the waters being repopulated the following summer from the sea. Should the region in which Bigelow found *Mnemiopsis* in such abundance in the Atlantic Ocean off the New Jersey coast be shifted even a mile or two eastward during some years, it would probably pass beyond the influence of the tidal ebb and flow through Barnegat Inlet and as a result few if any *Mnemiopsis* would be found in the Bay. Long continued easterly winds do bring to our shores forms which do not normally occur there but the effects of such winds and the currents produced thereby are doubtless only temporary.

No one knows the effects on the plankton of coastal waters which result from even slight shifts in the direction, and of changes in temperature or of salinity of the larger oceanic

currents. Until extensive oceanographic investigations are conducted along our coasts during every month of the year for a considerable period, we shall continue ignorant of most of the underlying factors which finally determine the abundance and distribution of many of the transient visitors to our coastal waters.

SUMMARY.

The occurrence and distribution of the three ctenophores, *Mnemiopsis leidyi*, *Pleurobrachia brunnea*, and *Beroë ovata* in New Jersey inland coastal waters are considered as affected by factors of the environment.

Pleurobrachia was observed twice, *Beroë* during a few days for three seasons, *Mnemiopsis* was seen daily for months at a time.

Evidence is presented which indicates that all three of these forms are casual visitors to the inland coastal waterways of New Jersey. *Beroë* and *Pleurobrachia* are found here only after the heat of summer is past, whereas *Mnemiopsis* appears in late spring or early summer and flourishes until late autumn or winter.

The remarkable power of temperature adaptation of *Mnemiopsis* is shown by the fact that in individuals taken in the winter the swimming plates continue to beat until frozen fast in the ice.

The three ctenophores are shown to be able to withstand salinities in the bays which are considerably below those of the ocean lanes from which the animals came. The conclusions of Mayer and of Bigelow in this connection are discussed.

A study of the food habits of *Mnemiopsis* reveals the fact that large numbers of bivalve larvæ may be destroyed by them. A distinct correlation is shown between the abundance of *Mnemiopsis* and the intensity of "sets" of oysters and of marine borers.

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